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SOME TRANSITIONAL ELASMOBRANCHS CONNECTING THE CATULOIDEA WITH THE CARCHARINOIDEA

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While engaged in the revision of the Order Galea outlined in my 'A Classification and Phylogeny of the Elasmobranch Fishes' recently published (Amer. Mus. Novitates No. 837, 1936), I came upon several species which aided materially in establishing the transition from the Catuloidea to the Carcharinoidea. These species have been difficult to classify because of their transitional nature, and have been assigned to various genera and have received various names in the recent literature. It is to settle these disputed points that this paper is presented.

The species in question are *Catulus torazame* of Tanaka, 1908, *Calliscyllium venustum* of Tanaka, 1912, *Atelomycterus marmoratus* of Garman, 1913, and *Triakis scyllium* of Müller and Henle, 1841. In order to establish comparisons I have selected three closely allied species whose characteristics do not vary from the established definitions: *Catulus retifer* of Garman, 1913, *Halaelurus burgeri* of Gill, 1861, and *Carcharinus milberti japonicus* of Schlegel, 1850. *Carcharinus* is a genus more familiarly known as the *Carcharias* of Cuvier, 1817, but Garman has recognized the priority claim of the name *Carcharinus* Blainville, 1816, and I have followed Garman's terminology wherever feasible. As this is an extremely stable genus, not all of the illustrations used have been selected from the species named.

I wish to express my appreciation to: Dr. Wm. K. Gregory, Curator of the Department of Ichthyology at The American Museum of Natural History, New York City, for the use of material from the Museum collections, and for research facilities at the Museum at all times; Dr. Naohide Yatsu and Dr. Negumi Eri who made available to me the necessary research facilities at the Imperial University of Tokyo and at the Marine Biological Laboratory at Misaki, Japan, and especially to Dr. Shigeho Tanaka for the valuable specimens supplied to me from his collections at the University; Dr. H. C. Delsman, and Dr. Verwey of the staff at the Laboratorium voor Het Onderzoek der Zee, Batavia, Java, in 1931, for material from the Laboratory collections, and for research facilities there.

For the convenience of the reader the characters of the suborders of the Order Galea, and of the superfamilies of the Suborder Carcharinida, are listed in parallel columns in Tables I and II. All of the species described here belong to the Suborder Carcharinida, and the transitional characters concerned connect the two superfamilies of that suborder, the Catuloidea and the Carcharinoidea. The terms catuloid and carcharinoid are used to refer to superfamily groups, and the terms catulid, triakid, and carcharinid, etc., to refer to family groups. The terminology is that used in my classification referred to above.

INTRODUCTION

The external characters of the elasmobranchs, including the teeth which are structurally homologous with the denticles, and those skeletal parts which are superficial in position and directly related to the external characters, are in a position to be more easily influenced by changes in the environment, and by feeding and swimming habits than are the more deeply seated internal characters. The superficial characters may be termed physiologic, therefore, in contrast to the phylogenetic. The physiologic characters will vary within closely related groups, even within a single genus, and many times will show parallel variations in groups of widely separate origin. The phylogenetic characters, on the other hand, have tended to show little change since the Jurassic and Cretaceous periods. Their development has been slow, but in definite directions, and they may be depended upon to establish true phylogenetic relationships even when the modern environment has caused apparently erratic variation in the physiologic characters. Thus we frequently find species in which the skeletal structures show an ancient origin while the superficial characters show advanced specializations to specific environments. Conversely, species are found which have advanced in their skeletal structure while retaining, or returning to, a primitive type of environment and thus showing primitive surface characters.

The sharp demarcation which I have shown in my suborder groupings between the spotted orectoloboid sharks and the spotted catuloid sharks is based on a group of correlated phylogenetic characters shown specifically in the vertebral centra, in the rostral cartilages, the pectoral fin base, the heart valves and the spiral valves. These small sharks have frequently been grouped together on the basis of parallel physiologic resemblances, whereas the structural demarcation was established during the Jurassic and has led through two diverse tendencies in development toward two wholly different groups of pelagic sharks.

Examination of a large number of specimens within the Suborder Carcharinida showed that the phylogenetic characters have more stability than the physiologic. Thus, the type of triradiate rostrum is invariable in the group, but the variation in the length and strength of the three rostral cartilages is correlated with the shape of the snout. There is no variation in the basic structure of the pectoral fin skeleton, in the arrangement of the radials on the basals, or, except in rare cases, in the number of segments in the radials, but the length of the radials varies with the shape of the fin. The diplospondylic vertebral structure is consistent within the entire group, but the secondary calcifications show so consistent a variation as to indicate an ancient origin. There is no variation in the basic structure of the skeletal support of the myxopterygia, in the number of stem elements or in the shape of the axial cartilages, but extreme and inconsistent variation occurs in the tendency for these cartilages to be rolled into a scroll, possibly indicating the recent development of these structures.

Thus it appears that the basic skeletal structures have been well established in the most primitive of these modern sharks, but that secondary skeletal structures have been later in establishing stability, and so give some hint as to the direction of development. This direction in the suborder under consideration appears to have been from a sluggish shore-dwelling type similar to the Jurassic catuloids toward a freer pelagic life as seen at its best in the swift and voracious carcharinids.

DISCUSSION

The seven species under discussion, *Catulus retifer*, *Catulus torazame*, *Halaelurus burgeri*, *Calliscyllium venustum*, *Atelomycterus marmoratus*, *Triakis scyllium*, and *Carcharinus milberti japonicus*, are shown in the order named in Fig. 1, and the structures referred to in this comparison are illustrated in the succeeding figures and listed in a comparative table (Table III). The first five species are catuloids and the last two are carcharinoids.

General Form

In the catuloids the body is characteristically shorter than the tail with the first dorsal fin either over or back of the pelvics. This condition is typical of fishes which travel slowly and attack prey by swishing the body from side to side with the tail as a lever. The mouth gapes in such forms are narrow, the teeth small and pluricuspid, and a possible protective camouflage is provided by the spotted and striped skins.

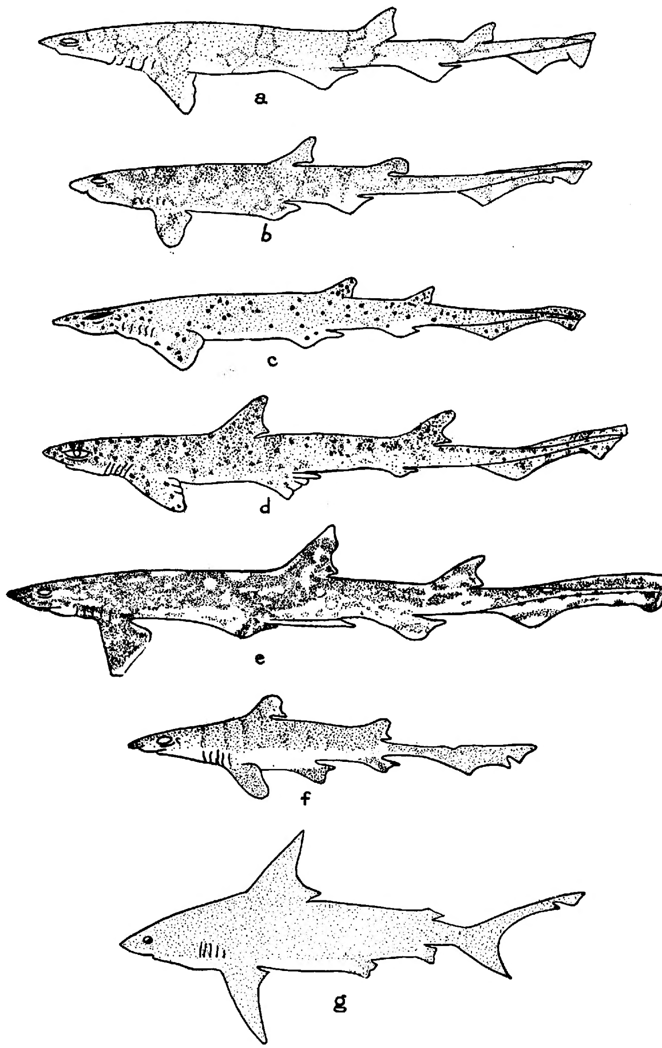

Fig. 1. *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Triakis scyllium; g, Carcharinus milberti japonicus.*

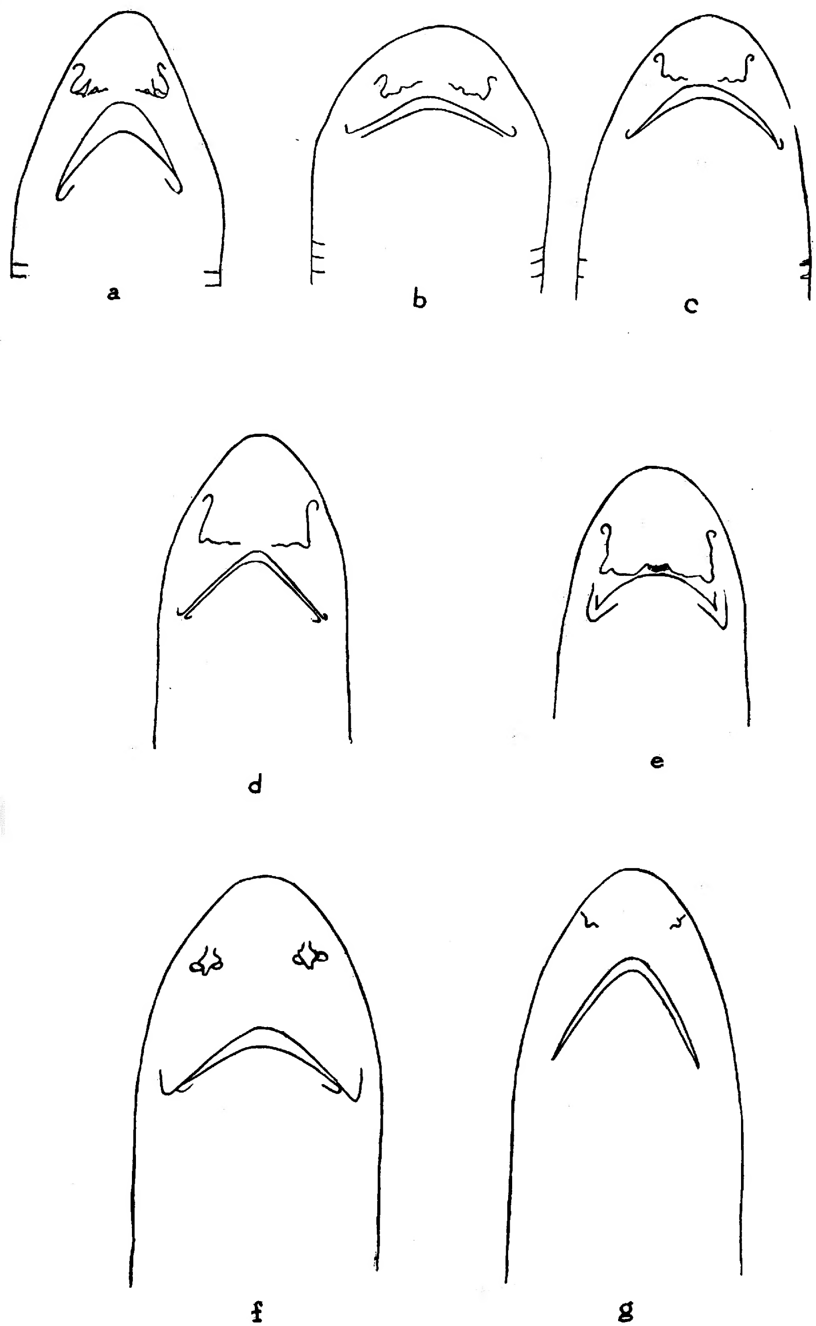

Fig. 2. Heads, ventral view: *a*, *Catulus retifer;* *b*, *Catulus torazame;* *c*, *Halaelurus burgeri;* *d*, *Calliscyllium venustum;* *e*, *Atelomycterus marmoratus;* *f*, *Triakis scyllium;* *g*, *Carcharinus milberti japonicus.*

In the carcharinoids the body is deepened anteriorly and the first dorsal fin is far forward. This is characteristic of pelagic swimmers and gives greater strength and swiftness. The mouth gapes are wide and farther from the snout than in the catuloids, and the teeth tend to become large and unicuspid. Characteristically the coloration is uniform, darker above and lighter below.

Triakis scyllium represents a transitional carcharinoid, bridging the gape between the littoral catuloids and the pelagic carcharinoids. The forward position of the dorsal fin and the deepening of the anterior region are characteristic and although *Triakis* is a small shark it is a swift swimmer and is found in quite deep waters. The mouth gape is intermediate and labial folds are retained. The teeth are small, numerous and three-cusped and may be an intermediate stage in the development of the unicuspid tooth, and the mouth is quite far from the snout.

Calliscyllium venustum parallels *Triakis* in several surface features and was classed as a species of *Triakis* by Garman in 1913, due to the forward position of the first dorsal fin which has always been looked upon as a determining character in the classification of sharks. There is, however, no corresponding deepening of the anterior region, the shark being peculiarly eel-like, and while it is found in quite deep waters it is a slow swimmer and has retained the mouth gape, teeth, and feeding habits of the littoral forms. It represents, therefore, a transitional stage in the tendency toward deep-sea life.

Atelomycterus is also an elongate shark which has paralleled the carcharinoids in some respects. It has, however, retained the posterior dorsal and has an even more shallow mouth gape than the typical catuloids. The nasal valves have reached the mouth to form nasoral grooves, a pronounced adaptation toward the feeding habits of grovellers. The life of *Atelomycterus* is a peculiar mixture of shallow- and deep-water habits. The shark is found exclusively among the coral reefs, chiefly of the Malay Archipelago where its eel-like body is adapted to the sinuous movements in and about the sharply cornered reefs, and its mouth to feeding upon the small animal life which frequents the coral reefs. This is not a transitional shark but represents the adaptation of a type far advanced in its internal structure to a peculiarly restricted environment.

Nictitating Fold

The presence of a nictitating fold or membrane in this group is peculiar in that it appears in no other group of sharks and in that

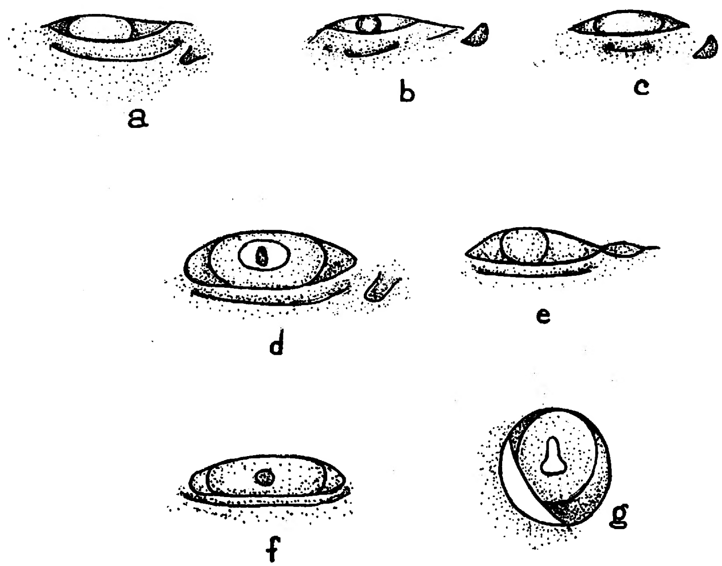

Fig. 3. Eye, spiracle and nictitating fold of: *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Triakis scyllium; g, Carcharinus milberti japonicus.*

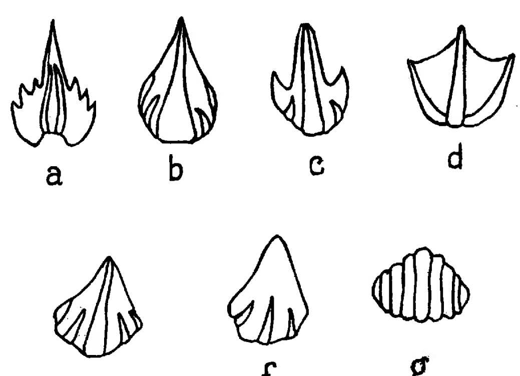

Fig. 4. Denticles from the dorsal surface of: *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Triakis scyllium; g, Carcharinus milberti japonicus.*

respect is correlated with the specific type of vertebral structure found in the suborder. This correlation between an internal skeletal structure and a surface structure is extraordinary and suggests the linkage of widely separate characters.

That the fold shows transition from a shallow fold to a complete third eyelid is shown in Fig. 3. This transition is not entirely correlated with the vertebral development, however, since *Triakis* and *Atelomycterus* retain the fold with the complete vertebral structure. It does show, nevertheless, that the more deeply seated skeletal structure reached its completion at an earlier time than the superficial one, and possibly indicates that the character is not one easily affected by changing environments.

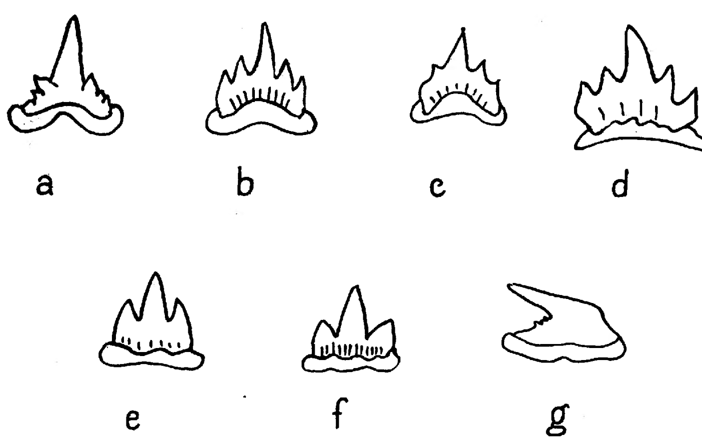

Fig. 5. Teeth, upper jaw of: *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Triakis scyllium; g, Carcharinus milberti japonicus.*

The length of the fold varies without any evident relation to the variations in the nasal valves. It appears to be shorter and less deep in the types adapted to the shallower waters, and to lengthen as the deeper waters are invaded, but this correlation is not absolute. The complete membrane is found only in the Carcharinidae where it sometimes functions as a third eyelid.

Denticles

The denticles (Fig. 4) show a tendency toward the flattened shell-like denticles of the pelagic forms in the smoothing out of the margin.

In the littoral forms the keels are sharp and incomplete, and the margin is decidedly lobed. In the more active swimmers the margin is decidedly less lobed and the keels are more complete.

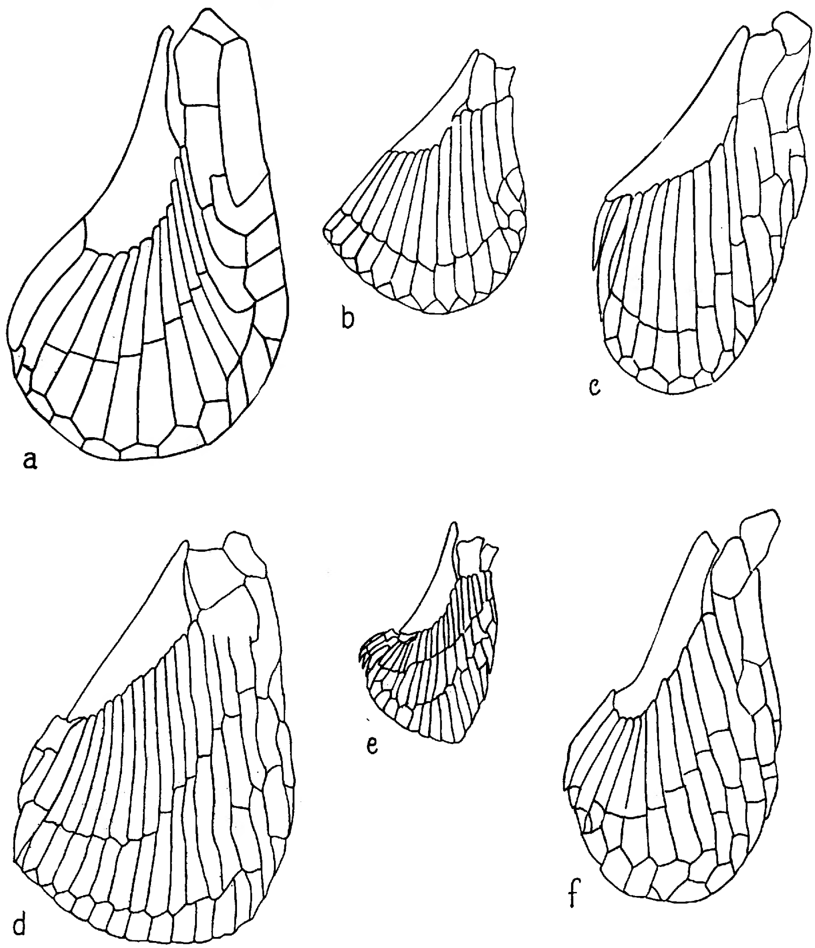

Fig. 6. Pectoral fin skeletons with propterygium on the right and expanded metapterygium on the left: *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Triakis scyllium.*

Rostrum

The triradiate rostrum is found consistently throughout the entire suborder and the only variation appears in the length and strength of the cartilages concerned. In the more pelagic forms these converge

into a point, but where the snout is depressed or broadened the front margin of the rostrum becomes squared. In no case does any break occur between the cartilages as in the orectolobid sharks.

PECTORAL FIN SKELETON

There is a consistent reduction of the propterygium throughout the suborder, but in all cases the radials are concentrated largely on the

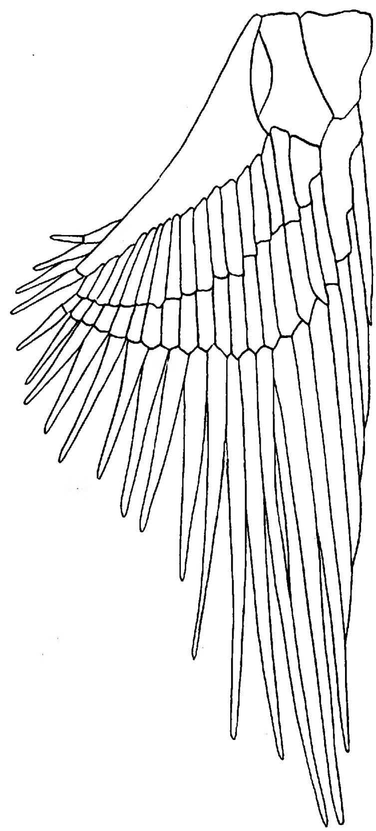

Fig. 7. Pectoral fin skeleton of *Carcharinus milberti japonicus*.

metapterygium. The radials are characteristically of three segments but in *Atelomycterus* some slight reduplication is apparent, correlating with the lengthened eel-like body. The length of the radials is determined by the length of the fin, and in *Carcharinus* the distal radials are greatly elongated to accommodate the long, falciform fins (Fig. 7). This is accomplished in the pelagic forms without reduplication.

Vertebral Centra

The secondary calcifications around the central double cone of the vertebral centra give the clearest picture of transition between the catuloids and carcharinoids (Fig. 8). The asterospondylic type is characteristic of the entire Order Galea, but in the Suborder Carcharinida the Maltese-cross type is so consistent as to provide a sharp line of de-

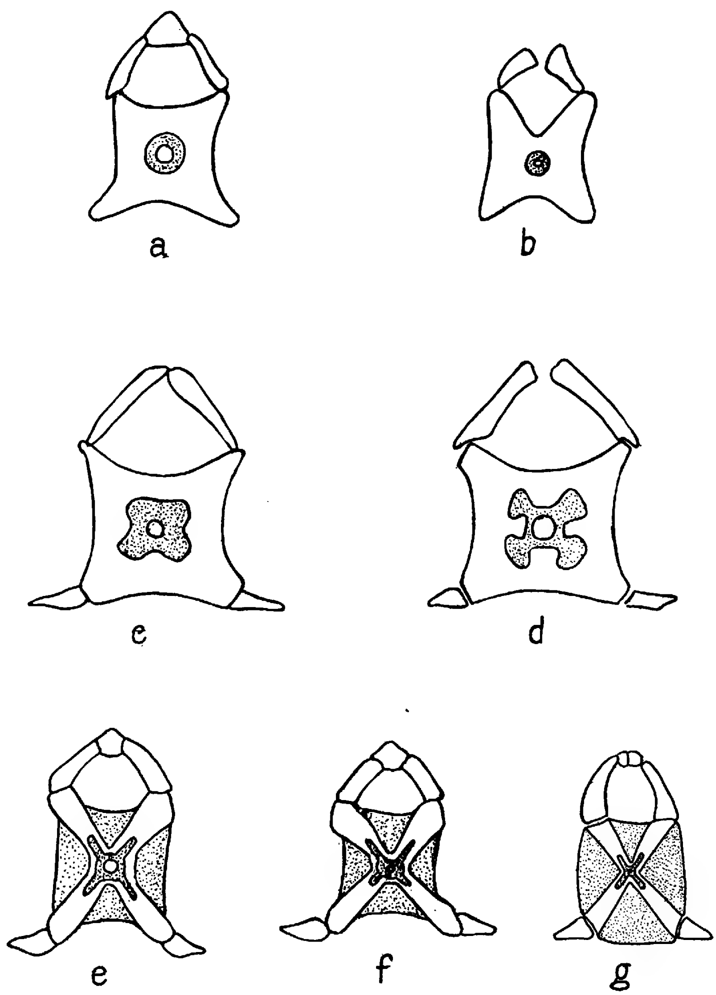

Fig. 8. Vertebral centra: *a, Catulus retifer* (Catulidae); *b, Catulus torazame* (Catulidae); *c, Halaelurus burgeri* (Halaeluridae); *d, Calliscyllium venustum* (Halaeluridae); *e, Atelomycterus marmoratus* (Atelomycteridae); *f, Triakis scyllium* (Triakidae); *g, Carcharinus sorrah* (Carcharinidae).

marcation between the two suborders. There are, however, certain primitive and transitional stages (Fig. 8 *a–d*) which I believe to have been retained from the Jurassic Period. This question is reviewed in the classification recently published (Amer. Mus. Novitates No. 837), where I have shown that the cases of asterospondylic vertebrae described in the literature on fossil forms are without doubt tectospondylic according to Tate Regan's modifications of Hasse's original definitions, and that what meager data exist concerning the vertebrae of the Jurassic catuloids show them to be of the cyclospondylic type. The Maltese-cross type was not established until the Cretaceous, when it was completed for all time.

Tate Regan believes the appearance of the cyclospondylic vertebrae in the modern catuloids indicates a retrogressive development returning to the primitive plan. The presence of cyclospondylic vertebrae, however, in the small Jurassic catuloids, *Pristiurus* and *Crossorhinus*, and the close resemblance of these fossil sharks to the modern genera preclude this possibility, and I believe the vertebral types in the modern catuloids to be a retention of a primitive phylogenetic character.

The transitional stages found in *Halaelurus* and in *Calliscyllium* are so pronounced as to indicate a definite tendency toward the formation of four calcified areas (Fig. 8 *c* and *d*), and the complete Maltese-cross type found in *Atelomycterus* (Fig. 8 *e*) indicates the completion of the type before the pelagic life was attempted. These phylogenetic tendencies are overshadowed by the adaptation of these modern forms to environments of widely differing types.

Believing the phylogenetic tendencies to be of more significance than the physiologic, I have divided the catuloid sharks into three families based on the cyclospondylic, the transitional, and the complete type of vertebra. Owing to the incomplete descriptions in the literature it has been impossible to assign all species with accuracy, but where the vertebrae have been either examined directly or described in the literature it has been possible to reassign certain species whose descriptions in Garman tally closely with the known types. In the case of genera of unknown vertebral type Garman's classification has been followed, but it is to be hoped that investigators in this field will add to the data now available by examining the vertebrae of those genera of doubtful assignation.

Spiral Valves

The spiral valves show a general tendency toward a reduction in the number of valves, culminating in the scroll type which is character-

istic of the pelagic carcharinoids. The retention of a reduced number of valves in *Triakis* is indicative of its transitional nature. The only case of duplication of valves appears in *Atelomycterus*, where the eel-like body probably accounts for the duplication. This is paralleled in the reduplication of radials in the pectoral fin. *Atelomycterus* is inconsistent in this respect, however, in that the reduplication is not carried out in the heart valves or in the cusps of the teeth. This inconsistency is found, also, in its mixture of feeding and swimming habits.

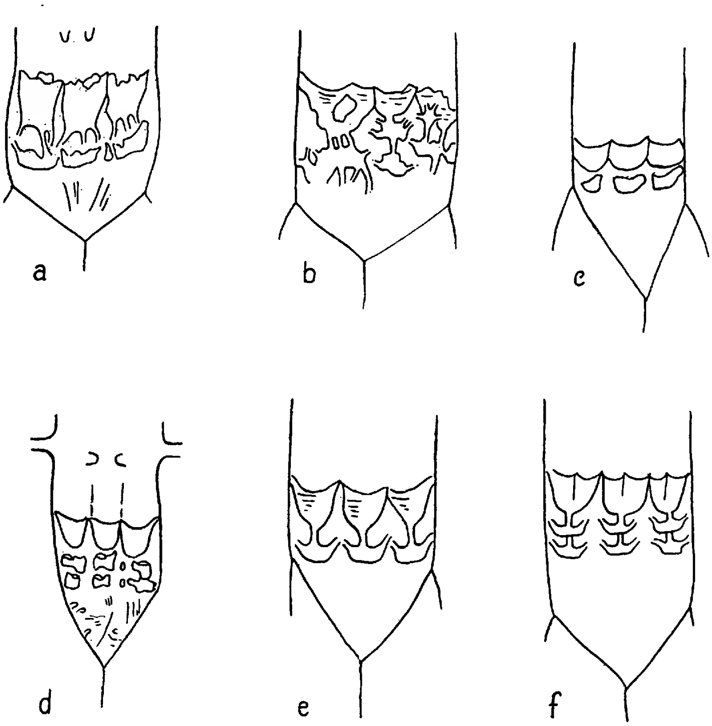

Fig. 9. Heart valves: *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Carcharinus sorrah.*

Heart Valves

The heart valves of the elasmobranchs, as shown in my recent paper (Am. Mus. Novitates No. 838), show a general tendency toward multiplication and progress from the primitive two-row type to three and even more rows. In the Suborder Carcharinida the progress is from two rows in the catuloids to three rows in the carcharinoids (Fig. 9).

Catulus torazame has a heart in which the transition from two to three rows is seen in progress. The valves frequently multiply in one row and then move down to form an additional row. In *Calliscyllium* the three valves are complete, but *Atelomycterus* which parallels *Triakis* in so many ways has retained the primitive two rows.

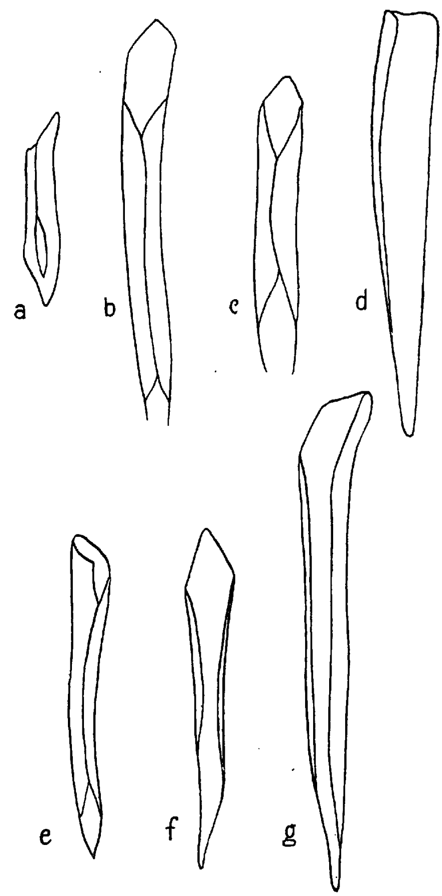

Fig. 10. Axial cartilages: *a, Catulus retifer; b, Catulus torazame; c, Halaelurus burgeri; d, Calliscyllium venustum; e, Atelomycterus marmoratus; f, Triakis scyllium; g, Carcharinus milberti japonicus.*

Myxopterygia

There is more variability shown in the axial cartilages of the myxopterygia than in any other vertebral structure. The basal elements and the general shape of the cartilages are entirely consistent through-

out the suborder, but the tendency to roll or unroll the marginal cartilages is strangely inconsistent. The earliest known sharks have no indication of any adaptation for internal fertilization, and it is probable that egg-laying with external fertilization preceded the condition characteristic of the modern sharks. It is possible, therefore, that the instability of the structural character of the axial cartilages is an indication of its comparatively late development.

In many of the catuloids the marginal cartilages are rolled into a tight scroll as in both species of *Catulus*, in *Halaelurus*, and in *Atelomycterus*. In *Calliscyllium*, *Triakis*, and *Carcharinus milberti japonicus* the margins are only slightly rolled in from the edge. This condition is not stable even in *Carcharinus*, however, some species having the marginals rolled and others open.

SUMMARY

Variation in the catuloids is so extreme as to make distinction even between genera difficult, and a study of the phylogenetic characters is of the utmost importance, therefore, in establishing relationships. The group is extremely stable in its phylogenetic characters, varying only in secondary structures, so that any important variation occurring in these structures may be considered of phylogenetic value.

The important variations include:

Length and shape of body (typically shorter than tail, occasionally eel-like);
Position of first dorsal fin (typically over or posterior to pelvics, rarely anterior);
Size and shape of all fins;
Armature on caudal (rare and primitive condition);
Size of eye and spiracle;
Length of nictitating fold;
Extent of labial folds;
Nasal valves and cirri (occasional nasoral grooves);
Dermal denticles;
Teeth (typically small, numerous, and five-cusped);
Heart valves (typically two rows, rarely three; phylogenetic);
Spiral valves (typically five to ten rows, tendency to reduction and to reduplication, phylogenetic);
Vertebral centra (cyclospondylic, intermediate, and rarely Maltese cross; phylogenetic);
Marginal axial cartilages of myxopterygia (typically rolled, tending to open);
Radials of pectoral fin skeleton (length, and rarely number of segments; phylogenetic).

The transitional species chosen are those which combine primitive catuloid characters with characters approaching or parallel to carcharin-

oid characters. The transitional characters are of more importance if concerned with the phylogenetic characters of which only the vertebral centra, heart valves and spiral valves vary to any considerable extent.

The characters of these species are listed below. The retained characters are those typical of the more primitive catuloids; the transitional characters are those which lead in the direction of the stable carcharinoid condition; the advanced characters those which parallel the carcharinoid condition, and the peculiar characters those which adapt the species to an environment not typical of either the catuloid or carcharinoid sharks.

Catulus torazame
- Retained characters:
    - Body short
    - First dorsal posterior
    - Nictitating fold rudimentary
    - Denticles incompletely keeled
    - Teeth five-cusped
    - Vertebral centra cyclospondylic (phylogenetic)
    - Marginal axial cartilages rolled into a scroll, loosely
    - Oviparous
- Transitional characters:
    - Heart valves forming a third row (phylogenetic)

Calliscyllium venustum
- Retained characters:
    - Denticles incompletely keeled
    - Teeth five-cusped
    - Oviparous
- Transitional characters:
    - Nictitating fold intermediate
    - Marginal axial cartilage open
    - Vertebral centra intermediate (phylogenetic)
- Advanced characters:
    - First dorsal anterior
    - Marginal axial cartilages open
    - Third row of heart valves complete (phylogenetic)
- Peculiar characters:
    - Body lengthened but not deepened anteriorly

Atelomycterus marmoratus
- Retained characters:
    - First dorsal posterior
    - Nictitating fold shorter than eye
    - Denticles with incomplete keels
    - Marginal axial cartilages coiled
    - Oviparous
- Transitional characters:
    - Denticles not lobed

Teeth three-cusped
Advanced characters:
Vertebral centra of Maltese-cross type (phylogenetic)
Peculair characters:
Body eel-like
Nasoral grooves
Slight reduplication of radials in pectoral fin skeleton (phylogenetic)
Reduplication in spiral valves

Within the carcharinoids, *Triakis scyllium* represents a transitional stage between the catuloid and the complete carcharinoid structure. This species has already been recognized by Leigh-Sharpe (1920) as transitional because of the presence of a retained clasper siphon and gland. My examination shows it to be transitional in many other respects also, and so decidedly leading to the stable condition of the carcharinoids that I have separated it from the specialized Galeorhinidae with which it has been associatedin theliterature and have made a new family, the Triakidae, to accommodate its transitional nature.

Triakis scyllium
Transitional characters:
Body spotted and striped
Spiracles small
Teeth three-cusped
Labial folds retained
Nictitating fold as long as eye
Denticles with incomplete keels
Spiral valves with few spirals (phylogenetic)
Advanced characters:
Body deepened anteriorly
First dorsal anterior
Vertebral centra of Maltese-cross type (phylogenetic)
Heart valves in three rows (phylogenetic)
Marginal axial cartilages open
Ovoviviparous
Carcharinus
Variable characters:
Spiracle minute or absent
Teeth serrated or smooth
Marginal axial cartilages coiled or open
Stable characters:
Color uniform, darker above
Body deepened anteriorly
First dorsal anterior
Nictitating membrane complete
Labial folds absent
Denticles completely keeled, shell-like

Vertebral centra of Maltese-cross type (phylogenetic)
Heart valves in three rows (phylogenetic)
Spiral valves of scroll type (phylogenetic)
Ovoviviparous

Carcharinus milberti (subspecies *japonicus*)
Spiracle absent
Teeth serrate, triangular on both jaws, lower teeth erect
Marginal axial cartilages open

In basing family divisions on phylogenetic characters several new families have been established, and new definitions compiled. These are listed below.

Catulidae

Catulidae of Garman, in part; Galeidae of Tanaka, in part; Scyliorhinidae of Regan, in part.

DEFINITION.—Body shorter than tail; anterior dorsal posterior to or just over pelvics; eyes large, lateral, nictitating fold shorter than eye; spiracles prominent; teeth small, pluricuspid, in several series; nasal valves nearer mouth than snout, occasionally reaching the mouth; denticles with prominent central keels, and lateral keels incomplete; vertebral centra cyclospondylic; heart valves in two rows; spiral valves with from five to ten valves.

CATULUS VALMONT, 1768

C. retifer Garman, 1913 (*Scyllium retiferum* Garman, 1881, *Scylliorhinus retifer* Jordan and Gilbert, 1883, Jordan and Everman, 1896; Goode and Bean, 1896; *Scyliorhinus retifer* Regan, 1908).

HABITAT.—Atlantic coast.

SPECIMEN.—Young male from the collection of The American Museum of Natural History, New York.

C. torazame Tanaka, March 15, 1908 (*Scyliorhinus rudis* Pietschman, March 19, 1908; *Halaelurus rudis* Tanaka, 1911, *H. torazame* Tanaka, 1912).

HABITAT.—Sagami Sea, Japan. Locally known as Torazame, tiger shark.

SPECIMENS.—Adult male and female (female with mature egg cases in oviduct) presented by Dr. Shigeho Tanaka from the collection of the Imperial University at Tokyo, Japan, 1930.

Halaeluridae, new family

Catulidae of Garman, in part; Galeidae of Tanaka, in part; Scyliorhinidae of Regan, in part.

DEFINITION.—Body shorter than tail; anterior dorsal over or anterior to pelvics; eyes medium, lateral, nictitating fold shorter than eye; spiracles prominent; teeth small, pluricuspid, in several series; nasal valves closer to mouth than snout, rarely reaching mouth; denticles

with prominent central keels, lateral keels incomplete; vertebral centra of intermediate types; heart valves in two to three rows; spiral valves in five to ten rows.

HALAELURUS GILL, 1861

Scyllium Müller and Henle, 1841.

H. burgeri Gill, 1861, Garman, 1913; *Scyllium burgeri* Müller and Henle, 1841; Schlegel, 1850; Bleeker, 1856; Duméril, 1865; Günther, 1870.

HABITAT.—Coastal waters from Japan to East Indies.

SPECIMENS.—Adult male and female presented by Dr. Shigeho Tanaka from the collection of the Imperial University of Tokyo in 1930.

CALLISCYLLIUM TANAKA, 1912 (in Family Galeidae)

Triakis Garman, 1913 (in Family Galeorhinidae).

C. venustum Tanaka, 1912; *Triakis venusta*, Garman, 1913.

HABITAT.—Sagami Sea, Japan. Locally known as Hyōzame, leopard shark.

SPECIMENS.—Adult male and female presented by Dr. Shigeho Tanaka from the collection of the Imperial University in Tokyo, 1930.

Atelomycteridae, new family

Catulidae of Garman, in part; Scyliorhinidae of Tate Regan, in part.

DEFINITION.—Body elongate; anterior dorsal posterior to pelvics; eyes large, lateral; spiracles prominent; nictitating fold as long as eye; teeth three-cusped; denticles with prominent central keels, lateral keels incomplete; vertebral centra of complete Maltese-cross type; heart valves in two rows; spiral valves numerous; radials of pectoral fin slightly reduplicated.

ATELOMYCTERUS GARMAN, 1913

Scyllium Bennett, 1830; *Scyliorhinus* Regan, 1908.

Scyllium marmoratum Bennett, 1830; *Scyllium maculatum* Gray and Hardwicke, 1832; Müller and Henle, 1841; Richardson, 1846; T. Cantor, 1849; Bleeker, 1852; Duméril, 1865; Günther, 1876; *Scyliorhinus marmoratus* Regan, 1908; *Atelomycterus marmoratus* Garman, 1913.

HABITAT.—Coral reefs of Malay Archipelago.

SPECIMEN.—Adult male presented by Dr. Verwey from the collection of the Laboratorium voor Het Onderzoek der Zee, Batavia, Java in 1931.

Triakidae, new family

Galeorhinidae of Garman, in part; Carcharidae of Regan, in part.

DEFINITION.—Body longer than tail, deepened anteriorly; first dorsal anterior to pelvics; eyes large, lateral; spiracles small; nictitating fold as long as eye; teeth small, numerous, three-cusped; denticles without prominent central keel, lateral keels incomplete; vertebral

centra of complete Maltese-cross type; heart valves in three rows; spiral valves few in number.

TRIAKIS MÜLLER AND HENLE, 1838

T. scyllium Müller and Henle, 1841; Duméril 1865; Günther, 1870; Ishikawa and Matsura, 1897; Snyder, 1900, Jordan and Fowler, 1903; Pietschman, 1908; Garman, 1913.

HABITAT.—Coastal waters of Japan.

SPECIMENS.—Male and female adults and young from open markets in Tokyo, Japan.

Carcharinidae Garman

Carcharidae Regan.

DEFINITION.—Body fusiform, deepened anteriorly; first dorsal anterior to pelvics; eyes small with more or less complete nictitating membrane; spiracles minute or absent; teeth large, few, with a single triangular cusp, with or without lateral serrations; denticles completely keeled, shell-like, without prominent central keel; vertebrae of complete Maltese-cross type; heart valves in three rows; spiral valves of scroll type.

CARCHARINUS BLAINVILLE, 1816

Carcharias Cuvier, 1817.

HABITAT.—Open oceans, universal.

Carcharinus milberti Jordan and Gilbert, 1883; *Carcharias Prionodon milberti* Müller and Henle, 1841. Subspecies *C. japonicus* Schlegel, 1850.

Specimen.—Fresh adult male, Misaki market, Japan.

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TABLE I.—SUBORDERS OF THE ORDER GALEA

ISURIDA	CARCHARIDA
Nictitating membrane absent	Nictitating fold or membrane present
Vertebral centra asterospondylic with secondary calcifications radiating, often branching in the calcified areas	Vertebral centra asterospondylic with secondary calcifications forming a Maltese cross or rudimentary
No rod-like calcifications in the uncalcified areas	Four rod-like calcifications in the uncalcified areas in Maltese-cross type
Spiral valves of ring type	Spiral valves of spiral or scroll type
Rostral cartilages triradiate open or closed	Rostral cartilages triradiate invariably closed
Pectoral fin skeleton	Pectoral fin skeleton
Radials on mesopterygium and metapterygium primitively equal	Radials mostly on metapterygium
Segments of radials typically more than three	Segments of radials three (rarely more)

TABLE II.—SUPERFAMILIES OF THE CARCHARINIDA

	CATULOIDEA	CARCHARINOIDEA
Dorsals:	Subequal	Subequal
First dorsal:	Posterior to pelvics (rarely anterior)	Anterior to pelvics
Nicitating membrane:	Fold present	Fold or membrane present
Spiracle:	Prominent	Reduced, minute, or absent
Nasoral grooves:	Absent or present	Absent
Labial folds:	Present	Absent or present
Denticles:	Central keel prominent	Central keel not prominent
	Keels incomplete	Keels incomplete or complete, shell-like
Teeth:	Small, pluricuspid	Large, unicuspid (rarely three-cusped or plate-like)
Series:	Several	1-several
Heart valves:	2 (rarely 3)	3 (rarely 2 or 4)
Spiral valves:	5–10 (rarely more)	2–4, or scroll type
Pectoral fin skeleton:		
Radials	Mostly on metapterygium	Mostly on metapterygium
Segments	3 (rarely more)	3
Rostral cartilages:	3 united	3 united
Vertebral centra:	Cyclospondylic, intermediate or rarely type	Maltese-cross type
Claspers:		
Siphon	Large	Large
Gland	Absent	Absent (rarely present)
Groove	Closed	Open or closed
Marginal axial cartilages:	Rolled (rarely open)	Open (rarely rolled)
Reproduction:	Oviparous	Ovoviviparous

TABLE III

	Catulus retifer	*Catulus torazame*	*Halaelurus burgeri*	*Calliscyllium venustum*	*Atelomycterus marmoratus*	*Triakis scyllium*	*Carcharinus milberti*
Body:	Short	Short	Short	Elongate	Elongate	Deepened anteriorly	Deepened anteriorly
Spots and stripes:	Present	Present	Present	Present	Present	Faint	Absent
Nictitating fold:	Slightly shorter than eye	Much shorter than eye	Much shorter than eye	Slightly shorter than eye	Shorter than eye	Equal length eye	Nicitating membrane complete
Spiracle:	Large	Large	Large	Large	Large	Small	Absent
Labial folds:	Present	Present	Present	Present	Present	Present	Absent
Nasoral grooves:	Present or absent	Absent	Absent	Absent	Present	Absent	Absent
Denticles:							
Apical margin	Lobed	Not lobed	Lobed	Lobed	Not lobed	Not lobed	Not lobed
Central keel	Prominent	Prominent	Prominent	Prominent	Prominent	Not prominent	Not prominent
Lateral keels	Incomplete	Incomplete	Incomplete	Incomplete	Incomplete	Incomplete	Complete
Teeth:	3–5-cusped	5-cusped	5-cusped	5-cusped	3-cusped	3-cusped	1-cusped
Heart valves:							
Number of rows	2	3, transitional	2	3	2	3	3
Spiral valves:	5–10	5–10	5–10	5–10	11–30	2–4	Scroll type
Vertebral centra:	Cyclospondylic	Cyclospondylic	Intermediate	Intermediate	Maltese cross	Maltese cross	Maltese cross
Myxopterygia:							
Marginal axial cartilages	Rolled	Rolled	Rolled	Open	Rolled	Open	Open